# ALIEN PLANTS IN CAMPBELL ISLAND'S CHANGING VEGETATION

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ABSTRACT

Eighty one alien plant species have been recorded growing on Campbell Island and a further six New Zealand indigenes may have also arrived recently through human agencies. Four classes of aliens were identified. Ten "widespread naturalized" species are recognized with *Cerastium holosteoides, Poa annua, Stellaria media, Sagina procumbens, Poa pratensis, Festuca rubra* and *Agrostis tenuis* being most consistently distributed, as indeed they are throughout the subantarctic. A further 19 naturalized species are confined to the coves and valleys immediately surrounding the head of Perseverance Harbour, and form a class of "restricted naturalized aliens". Twenty-two "persistent" and 30 "transient" aliens are, or were, restricted almost exclusively to past or present occupation sites.

Dispersal, establishment and invasion by the aliens available from the total species pool, as reflected by their current distribution, is discussed in relation to five historical phases (of which pastoral exploitation was the most critical), the adaptations of the migrants and the defensive strategies of the native vegetation.

Sheep experimentally fed on important indigenous species demonstrated preferences for young *Polystichum* fronds, *Poa foliosa, Anisotome latifolia* and *Chionochloa antarctica* over *Poa litorosa* and *Bulbinella rossii* which presently codominate former *C. antarctica/P. foliosa* tussock grasslands.

The resilience of the native species is also indicated by the failure of any alien plant so far introduced to become noxious, in the sense of threatening the place of an indigene. It is only grazing mammals and their human beneficiaries who have drastically transformed the natural vegetation.

It is suggested that with the removal of these influences the artificially disturbed communities will slowly develop into new climax associations in which a group of less than 24 proven aliens will become integrated while the remaining c. 60 introduced species will form transient or persistent populations around human settlements.

## INTRODUCTION

### GENERAL

An alien plant species is one which is foreign to a locality. In this paper the strictly human introductions (direct or

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indirect) are distinguished from migrant plants generally, all of which may be considered initially alien.

This is a documentation of the history of the numerically large exotic component of Campbell Island's flora, a nevertheless relatively inconspicuous element of the vegetation. It represents 39% of the total vascular flora (209 spp., C.D. Meurk and D.G. Given in prep.). It is timely to make such an assessment since with the declaration of Campbell Island's Reserve status in 1954, and with the start made in 1970 to eliminate the feral sheep population (Taylor *et al.* 1970), a declining role is envisaged for the adventive flora.

The four classes of alien species employed by Walton and Smith (1973) in the South Georgian context (this island lies 200 km east of Tierra del Fuego) were adapted for use on the more modified Campbell Island. The classes are:

transient aliens - one or few individuals surviving one or two years in artificial habitats;
persistent aliens - individuals or a small population surviving many years in artificial habitats or in seral communities;
restricted naturalized aliens - one or few small populations which maintain themselves or have spread, usually vegetatively, into seral communities of limited areas;
widespread naturalized aliens - numerous, usually freely seeding populations which have spread and successfully competed with the native species over at least half the Island.

Brief consideration is given to intrinsic and induced trends in the vegetation relevant to understanding the impact of exotic influences. In a palatability experiment to test assumptions about the effects of grazing on the vegetation, pairs of sheep, penned on Campbell Island, were given free access to cut bundles of fresh-weighed leaves of five important native plants. The tied bundles were suspended above the ground against the pen wall. The preferences of the sheep were deduced from their feeding behaviour, observed from a hide, and from the fresh weights of the plant residues left after about a half-hour of feeding. The experiment was run four times, with a ram and ewe on the first occasion and a pair of ewes thereafter. All had been in captivity for several weeks and were left unfed for some hours prior to the experiment. Analyses of variance were performed on arcsin transformed percentage data.

## PHYSIOGRAPHY AND CLIMATE

The eroded volcanic cone of Campbell Island (Fig. 1) lies some 600 km south of Stewart Island and is a similar distance from the Antarctic Convergence, despite its southerly position (52°33'S, 169°8'E). The island covers an area of about 10 900 ha and rises to an altitude of 569 m.

Although the climate is overwhelmingly oceanic (mean daily range and extreme range of monthly means are c. 5°C), zonally the island is alpine, with sea level closely corresponding to tree limit conditions (mean January temperature = 9.3°C, De Lisle 1965). Strong salt-laden winds, high humidity, weak

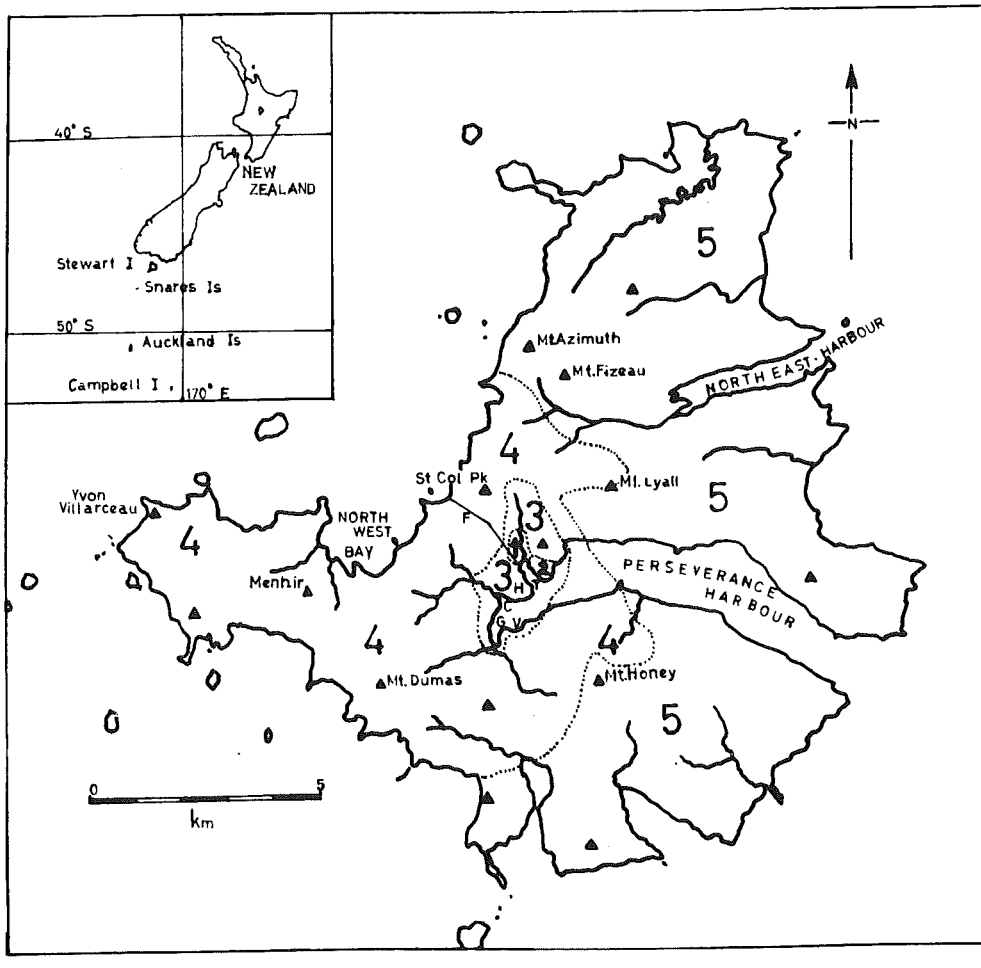


Fig. 1. Physiography and distributional zones of alien plants of Campbell Island (1970-76). Each higher numbered zone subsumes lower numbered zones except for the contiguous zones 1 ("Cape Expedition" area) and 2 (Beeman Point Meteorological Station area). T = Tucker Cove; C = Camp Cove; G = Garden Cove; V = Venus Cove; H = Homestead Ridge; F = Fence line.

diffuse light, uniformly cool temperatures and peaty soils characterise the environment.

## VEGETATION

From early accounts (Hooker 1844, Norman and Musgrave 1866, M'Cormick 1884, Cockayne 1903) and photographs (Dougall 1888b) and by studying remnants of unmodified associations, a reconstruction of the pristine vegetation is possible. Three

zones and several intrazonal communities can be inferred:

1. subalpine *Dracophyllum*-dwarf forest, restricted to sheltered harbour heads and deep gullies;

2. low alpine zone up to 300 m, dominated by stands of snow grass tussock (*Chionochloa antarctica*) actually or potentially associated with shrubs which today predominate up to 200 m in sheltered places;

3. high alpine zone, characterised by wet rush-herbfields.

Littoral/maritime, sedge-flush, shrub-flush, tussock-cushion ("lane"), wet-cushion, fellfield, rockledge, peat slip and biotic (nesting sites, wallows etc.) communities form(ed) mosaics with the zonal types.

Penetration of aliens into these communities would have been slow until farming began in 1895. Scrub cutting, fire, grazing stock and the broadcast of pasture plants devastated the low alpine zone where the fresh palatable growth of the burnt snow grass provided the chief source of fodder. Mark (1965) has demonstrated that mainland snowgrasses suffer no permanent damage from burning but the pressure of associated grazing is critical. As a consequence, *C. antarctica* grasslands have been largely supplanted by short open tussock-meadows physiognomically dominated by *Poa litorosa, Bulbinella rossii,* herbs, ferns, cushions, cryptogams and/or eroded peat. This is analogous to the replacement of tall tussock on the New Zealand mainland by silver (*Poa laevis*) and fescue short tussock associations.

Where the secondary succession has been retarded by exposure or grazing pressure, tussock growth is suppressed which results in a seral *Bulbinella*-turf meadow. These induced *P. litorosa/B. rossii* meadows must not be confused with the strictly maritime large statured *P. litorosa* tussock grasslands which must have predated the farming. However they have probably been an important source of seed for the developing meadows.

## HISTORY OF EXOTIC INFLUENCES ON THE VEGETATION

With the discovery of Campbell and Macquarie Islands in 1810 there was a brief revival of the Australasian sealing, and later whaling, trades. Although more than 111 ships were known to have been in these waters up to 1830, the greatest activity probably centered on the more lucrative sealing grounds of Macquarie Island (McNab 1907, Kerr 1976). Nevertheless, Campbell Island was an occasional port of call where ships en route to England would take on water and gather wood for fuel (Ross 1847, McNab 1907). Certainly the number of hut remains and gravestones reported around the coves of Perseverance Harbour, Northeast Harbour and Northwest Bay, throughout the nineteenth century, indicated continual localised occupation by sealing and whaling gangs, some of whom were callously left to fend for themselves for months and even years (Kerr 1976). The sealer's boots, clothing and building materials undoubtedly harboured the seeds of exotic plants and rats would have become established very early.

Hooker (1847) described the alarming way in which fires spread for miles through dried-out snowgrass on the Auckland

Islands and Armstrong (1868) reported the making of "fires everywhere" in the same species on Campbell Island in the hope of attracting any sheltering castaways. The French were responsible for two major fires in 1874 (Bouquet de la Grye 1882).

In 1865 one ash, six oaks, and six elms were planted by a crew member of one of the many "search and rescue" ships that visited the southern islands around this time (Norman and Musgrave 1865). A French party planted potatos and other vegetables at Garden Cove in 1873, in preparation for the following year's "Transit of Venus" expedition, but only a few stunted cabbages survived (Filhol 1885). Attempts at growing vegetables were probably many and, in view of the plight of some early inhabitants, largely frustrated (Spense 1968, J. Timms, a former shepherd recalled success only with lettuces, N. Judd pers. comm.). Better results have been achieved more recently on imported topsoil under semi-artificial conditions by Sorensen and subsequent enthusiasts in the Meteorological Service (Meurk 1975, Kerr 1976).

Although Buchanan (1884) made the first definite record of an adventive plant - a *Chenopodium* sp. - it was some time before others were reported despite the often deliberate though largely unsuccessful introductions that continued. Dougall (1888a) mentioned that grass seed was sown in Tucker Cove and gums, firs, wattles and scotch broom were planted. Kirk (1891) claimed that Stewart Island Maoris had obtained heather from Campbell Island some years previously, but by 1953 it had almost died out (Meurk 1975, Kerr 1976).

Throughout the latter part of the nineteenth century sheep, pigs, goats and wildfowl were liberated, but they never became established as on the Auckland Islands. With growing interests in subantarctic sheep farming a feasibility study was commissioned in 1894, for which J.P. Joyce MP reported that ryegrass sown six months earlier had come up and had taken good hold of the soil (Kerr 1976). In 1895 the landing of building materials and 300-400 sheep heralded the farming period although it was not until the turn of the century that stock numbers had reached 2 000 (Wilson and Orwin 1964). Cockayne (1903) estimated that sheep occupied half of the island and was impressed by the destruction of scrub, snow tussock and subantarctic endemics brought about by fire and grazing. He did however refer to the small number of naturalized plants, but did not list them.

In 1906 the Government rebuilt the castaway depots for the last time. Cattle, sheep and goats were released and seeds of exotic plants sown (Kerr 1976). During their 25 year tenure the resident shepherds were more assiduous in their attempts to improve the pastures, by cutting scrub, burning the rank cover and then scattering grass and clover mixtures. Judging by the current distribution of chewing's fescue (*Festuca rubra*) and brown top (*Agrostis tenuis*) this occurred chiefly in the St Col ridge, Mt. Honey cirque, Mt. Dumas and Yvon Villarceau areas. However most of this "improvement" apparently did not take effect until after Laing's visit.

Laing (1909) published the first inventory of adventive species from a 1907 collection made "on the beach near the

homestead at the edge of a little water-course", but added that "introduced plants at present show but little sign of spreading and are still very few in number". His list included: Yorkshire fog (*Holcus lanatus*), cocksfoot (*Dactylis glomerata*), perennial ryegrass (*Lolium perenne*), sweet vernal (*Anthoxanthum odoratum*), N.Z. flax (*Phormium tenax*), sheep's sorrel (*Rumex acetosella*), white clover (*Trifolium repens*), mouse-eared chickweed (*Cerastium* sp.), common chickweed (*Stellaria media*), catsear (*Hypochaeris radicata*), and heather (*Calluna vulgaris*). Laing also recalled that the head shepherd "had some specimens of rata (*Metrosideros lucida = umbellata*), perhaps 2 ft high, growing inside a ring fence of dead *Dracophyllum* branches". The shepherd confirmed that they were from the mainland and Laing doubted they would survive. Petrie (1909) recorded "*Festuca ovina*", later regarded by Zotov (1965) as an aberrant form of *F. rubra* Cheeseman (1909) added *Poa annua*, but commented that little attention was paid to adventives.

Sheep numbers peaked at around 8000 between 1906-1916 (Wilson and Orwin 1964), but with exhaustion of the indigenous pasture sheep productivity declined and the whole business (including the supplementary whaling operations which concluded in 1913) foundered as the "Great Depression" loomed. When the run was abandoned in 1931 less than 4000 sheep remained. This number gradually declined to 1000 in 1961, but rose sharply to 3000 by 1969 (Taylor *et al.* 1970). This natural increase has continued in the population south of the extermination fence line (see below), whereas the small herd of cattle still inhabiting the southwest part of the Island has remained constant (Taylor *et al.* 1970, P.R. Wilson and P.J. Dilks in prep.).

The establishment of the wartime "Cape Expedition" in Tucker Valley (1941-45) and the subsequent resiting of the Meteorological Station at Beeman Point (1957) may prove to be the last chapters in the history of human interference with Campbell Island's vegetation. Sorensen (1951), Godley (1969), and Meurk (1975) between them added a further 36 species to the adventive flora. Only 13 of these (all recorded by Sorensen) could be considered more than transient, which suggests that the important aliens were all established very early, but that knowledge of the florula was mainly limited by the infrequency of collectors.

The history of human interference with Campbell Island's vegetation can be conveniently divided into five overlapping phases in which moderate or moderating influences have alternated with deteriorating conditions:

1. 1810-1913; exploitation of native fauna, English and French expeditions, intermittent and local repercussions for the vegetation whose natural order was scarcely affected;

2. 1895-1931; exploitation of pastoral resources, N.Z. expeditions, widespread severe damage to the low alpine zone, decimation of palatable species;

3. 1931-c.1960; natural decline in sheep numbers, increasingly dramatic secondary succession of *P. litorosa* and scrub in low alpine;

4. c.1960-1970; minor expansion of sheep population, but continuing encroachment of scrub into tussock meadows:

5. 1970-?; removal of sheep from north of fence erected between Tucker Cove and western cliffs (Fig. 1), continuation of trends in (4), succession in *Bulbinella* - turf meadows involving exotic grasses and indigenous palatable species, possible eventual elimination of all introduced mammals.

Superimposed on these phases were four events of strictly local significance: a) 1873-4; French "Transit of Venus" settlement in Venus Cove and preparation of a vegetable garden in Garden Cove; b) 1895-1931; farm buildings and holding paddocks established on Homestead Ridge; c) 1941-57; "Cape Expedition" and Meteorological Station encampment in Tucker Valley, first continuous long term botanical studies; d) 1957-?; resiting of Meteorological Station at Beeman Point, growing botanical activity which has increased opportunities for intercepting sporadic appearances of transient weeds. All of these settlements, including some others in Northwest Bay, Northeast Harbour and Camp Cove, would have provided transient habitats for many of the species which have recently become recognized members of the alien flora. Reclamation, by the native vegetation, is still progressing at the old Tucker Valley camp whereas little botanical evidence remains of the Venus Cove occupation.

Fig. 2 depicts the interactions of the historical phases, the impact on the vegetation, the results of botanical exploration and the introduction and penetration of exotic plants. The ecological impact curve was devised by assuming stock gains were proportional to impact, whereas stock losses were assigned a negative impact equal arbitrarily to half the numerical loss. A major settlement was given a rating of 100 stock units.

## RESULTS

### I THE ALIEN PLANTS

#### General

Table 1 is an inventory of all adventive species that have been reported growing on Campbell Island in the open, although in some cases within the shelter of protective fences. Voucher specimens for all species (except *Metrosideros umbellata*) are held at CHR, CANU, WELT or OTA herbarium (see Godley 1969 and Meurk 1975). The species are arranged according to the earlier defined alien classes. Each name is followed by symbols indicating reproductive strategy, observed flowering success/probable means of introduction/ability of seed to germinate after passing through stock gut and distribution by geographical zone number as depicted in Fig. 1.

Apart from a few New Zealand native introductions and one from North America (*Epilobium ciliatum*) all the others are well known European weeds, pasture plants or vegetables.

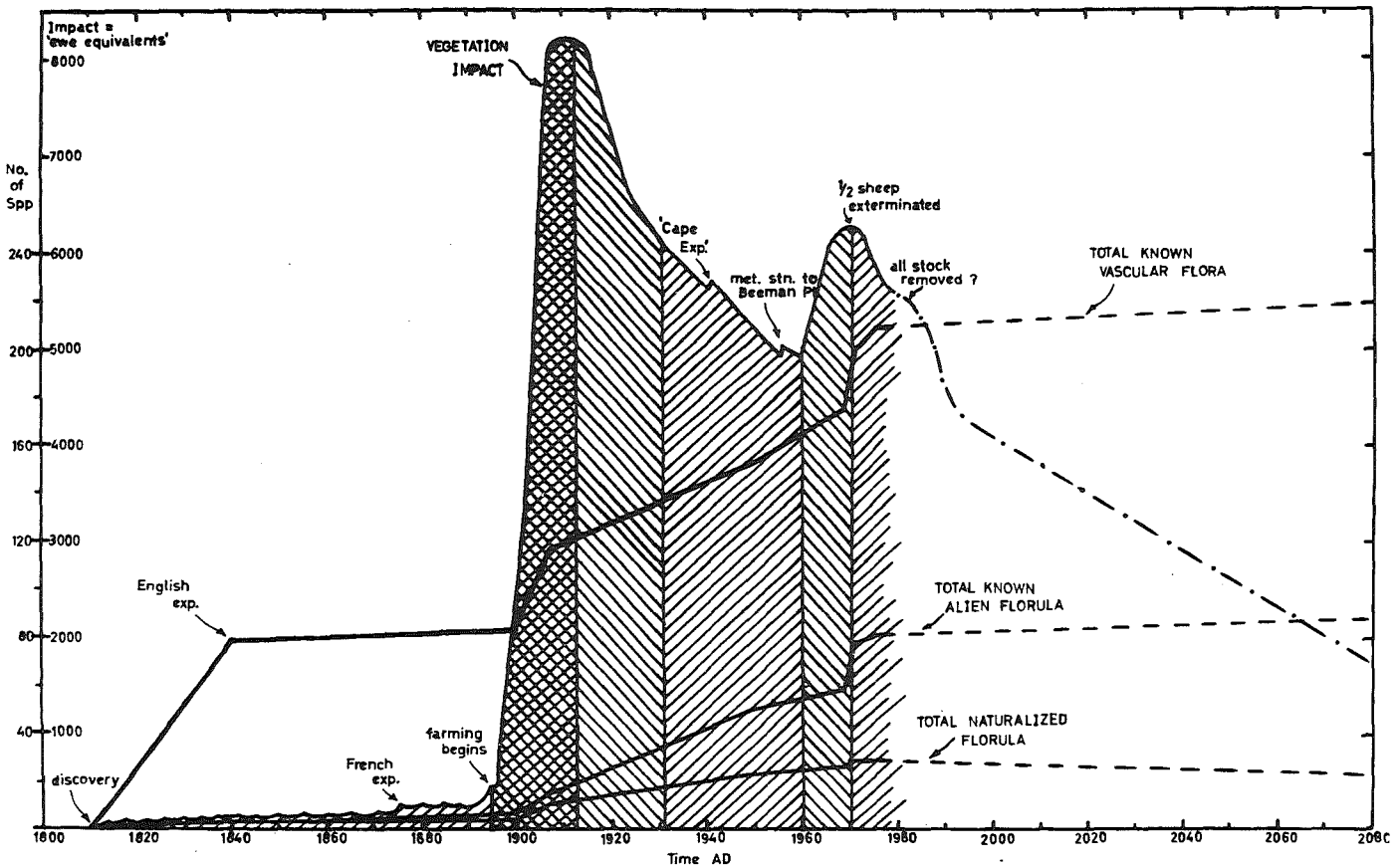


Fig. 2. Graphical depiction of the relationships between historical phases on Campbell Island, ecological impact, botanical knowledge and the status of the alien flora. Alternating hatching patterns represent the five overlapping historical periods described in the text.

TABLE 1. LIST OF CAMPBELL ISLAND ALIEN PLANT SPECIES SEGREGATED INTO FOUR GEOGRAPHICAL/TEMPORAL CLASSES. Suffixed notations indicate reproductive strategy: A = annual/biennial, P = perennial, N = never observed flowering; probable means of introduction/dispersal: F = introduced as vegetable, ornamental cultivar or as some commercial crop, G = broadcast as pasture species, C = contaminant in seed mixtures, H = possibly introduced on clothes, boots, building or packing materials, on animals or in imported soil, I = known to survive passage through animals intestine; and geographical zone number (Fig. 1): (1), (2) = confined to settlement areas, (3) = confined to head of Perseverance Harbour vicinity, (4) = confined to intensively farmed area, (5) = dispersed over the whole island.

TRANSIENT ALIENS

*Allium cepa* A/F/(1)
*Anagallis arvensis* A/HCI/(1)
*Aphanes microcarpa* AN/HCI/(1)
*Avena sativa* A/HCI/(1)
*Beta vulgaris vulgaris* P/F/(2)
*Betula papyrifera* PN/F/(2)
*Brassica oleracea capitata* P/F/(2)
*Bromus brevi-aristatus* A/H/(1)
*Chenopodium album* AN/HCI/(1,2)
*Coronopus didymus* AN/H/(1,2)
*Daucus carota* AN/FI/(2)
*Epilobium ciliatum* P/H/(1,2)
*Epilobium montanum* P/H/(1)
*Fumaria officinalis* A/HCI/(1)
*Geranium pusillum* A/HCI/(2)
*Juncus articulatus* P/H/(1)
*Lactuca sativa* AN/F/(2)
*Leontodon taraxacoides* P/H/(1)
*Lolium multiflorum* A/H/(2)
*Metrosideros umbellata* PN/F/(3)
*Polygonum aviculare* AN/HI/(1)
*Polygonum convolvulus* AN/HC/(1)
*Polygonum persicaria* AN/HCI/(1,2)
*Raphanus sativus* AN/F/(2)
*Solanum nigrum* AN/H/(1)
*Spergula arvensis* AN/HCI/(1)
*Trifolium dubium* A/HC/(1)
*Ulex europaeus* PN/HC/(1)
*Veronica agrestis* A/HI/(1)
*Veronica persica* A/H/(1,2)

PERSISTENT ALIENS

*Calluna vulgaris* P/F/(3)
*Capsella bursa-pastoris* A/HCI/(1,2)
*Cardamine hirsuta* A/H/(1,2)
*Cynosurus cristatus* P/GH/(1,3)
*Digitalis purpureus* A/H/(1,2)
*Fragaria x ananassa* P/F/(1,2)
*Hypericum androsaemum* P/?I/(3)
*Juncus effusus* P/CH/(3)
*Leucanthemum vulgare** P/HCI/(2)
*Lolium perenne* P/GH/(1,2,3)
*Phleum pratense* P/G/(1)
*Picea sitchensis* PN/F/(3)
*Plantago lanceolata* P/CHI/(1,2,3)
*Prunella vulgaris* P/CI/(1,4)
*Ribes nigrum* PN/F/(1)
*Sarothamnus scoparius* P/FH/(1,2)
*Solanum tuberosum* PN/F/(1,2,3,4)
*Sonchus oleraceus* A/HCI/(1,2)
*Stellaria graminea* P/H/(1)
*Trifolium pratense* P/GH/(1)
*Veronica arvensis* A/HI/(1,2)
*Vulpia bromoides* A/CH/(1,4)

* formerly *Chrysanthemum leucanthemum*

NATURALIZED SPECIES

RESTRICTED ALIENS

*Achillea millefolium* P/HCI/(1,2)
*Agropyron repens* P/HC/(1,2)
*Alopecurus geniculatus* P/C/(1,3)
*Anthoxanthum odoratum* P/GC/(3,4)
*Arrhenatherum elatius* P/G/(3)
*Bellis perennis* P/CH/(1,2)
*Dactylis glomerata* P/G/(3)
*Hypochaeris radicata* P/CH/(3)

WIDESPREAD ALIENS

*Agrostis tenuis* P/GC/(4)
*Cerastium holosteoides* P/CHI/(5)
*Festuca rubra commutata* P/G/(5)
*Holcus lanatus* P/GC/(4)
*Poa annua* AP/CI/(5)
*Poa pratensis* P/G/(5)
*Poa trivialis* P/G/(4)
*Sagina procumbens* P/HCI/(5)

TABLE 1 (continued)

*Juncus bufonius* A/HI/(1,2)
*Lamium purpureum* A/HI/(1)
*Lotus uliginosus* P/HC/(1)
*Mimulus guttatus* PN/HC/(1)
*Phormium tenax* P/F/(1,3)
*Ranunculus repens* P/HCI/(1,2,3)
*Rumex acetosella* P/CI/(3)
*Rumex crispus* P/CHI/(3)
*Rumex obtusifolius* P/CHI/(3)
*Sonchus asper* A/C/(3)
*Taraxacum officinale* P/HCI/(2,3,4)
*Stellaria media* A/CHI/(5)
*Trifolium repens* P/G/(1,3,4)

Transient aliens (31 spp.)

Annuals comprise 70% of the transient species and of these 50% have never been observed flowering. There are six garden vegetables on the list which have probably had a long and unsuccessful history on the island. Another two are failed ornamentals. Of the remainder the only perennials are two *Epilobium* spp., *Juncus articulatus, Leontodon taraxacoides* and gorse (*Ulex europaeus*), but most of the observed plants were taken as reference specimens as has been the case with many of the transients (Godley 1969, Meurk 1975).

Representatives of this group have always been found close to human habitation (zones 1 and 2 in Fig. 1). It is probable that about 73% of them were accidentally imported on muddy boots, clothes, stock, building and packing materials or garden soil (see Sorensen 1951).

Persistent aliens (22 spp.)

Only 27% of these are annuals/biennials and they have all been observed flowering, whereas over 80% of the perennials have also flowered. Some have limited powers of vegetative spread (e.g. strawberry *Fragaria x ananassa*), potato (*Solanum tuberosum*), *Trifolium pratense* , heather, self heal (*Prunella vulgaris*), and the grasses). Some species classed here have not been seen recently, but because of their generally long histories in the wild are warranted a status above transience. These include heather, foxglove (*Digitalis purpureus*, recurs on old sites of disturbance), tutsan (*Hypericum androsaemum*, a puzzling record, the plant being removed to check any spread), *Juncus effusus* (recurring, but not seen in 1975/76), *Leucanthemum vulgare* (observed for the two consecutive years of 1970/71, but absent by 1975), *Plantago lanceolata* (recurring on old occupation sites but sometimes remote from current disturbance; a large flowering patch was seen in 1975/76 near the Meteorological Station), selfheal (disappeared from southwest part of island between 1971 and 1975), broom (*Sarothamnus scoparius*, large flowering bushes removed several times in past decade), potato (reported to be growing in Northwest Bay in 1945), *Stellaria graminea* and *Trifolium pratense* (both disappeared from Tucker Valley between 1971 and 1975). Detailed information concerning these species is contained in Oliver and Sorensen (1951), Sorensen (1951), Godley (1969) and Meurk (1975).

*Vulpia bromoides* was recorded for the first time from Tucker Valley in 1971 (Meurk 1975), but in 1976 a surprising find was made on a sheep track c. 100 m above Perseverance Harbour at the foot of Mt Honey. Perennial ryegrass has had more chequered fortunes. It has been reported numerous times since the beginning of the century as both deliberate introductions and spontaneous occurrences, but although Sorensen (1951) and Joyce (in Kerr 1976) claimed it was spreading, only a few plants have been seen around the Meteorological Station and Tucker Camp in recent years.

The lone spruce tree (*Picea* sp.) is included here, despite its assured longevity, because of its failure to reproduce or even bear cones. Oliver and Sorensen (1951) said the spruce "was not recorded by 1907 party, although it must have been present then". Mr J. Timms (Shepherd), in an interview with N. Judd (pers. comm.) did not recall seeing it in 1912. Certainly, linear regressions fitted to its growth parameters support a post-1910 planting (Meurk 1975).

Some of the persistent species are common along the walkways around the Meteorological Station (e.g. shepherd's purse (*Capsella bursa-pastoris*) - perhaps an indicator species of this class; *Cardamine hirsuta; Sonchus oleraceus;* and *Veronica arvensis*). However in general, this category could be regarded as headed for extinction, at least without continued seed supply and disturbance of the ground.

Restricted naturalized aliens (19 spp.)

The three annuals all flower regularly. Many of the other species are aggressively vegetative, particularly the grasses, *Mimulus guttatus, Ranunculus repens,* yarrow (*Achillea millefolium*) and *Lotus uliginosus.* The old flax clumps (probably planted last century) look extremely vigorous, but have not spread from their original localities unassisted (Meurk 1975), although Oliver and Sorensen (1951) did note some young plants. In 1975/76 the flax flowered and developed capsules for the first time on record, apparently due to induction in the previous exceptionally mild summer*. Flax was a frequent bartering commodity during the middle of last century and helped to offset the effects of a flagging seal trade. It was introduced to various subantarctic islands to test its growth potential and to supply forgotten hunters with raw materials (McNab 1907).

Included in this category are species with either a very firm grip on one or a few sites (mainly around the "Cape Expedition" camp as with the above mentioned five species and including twitch (*Agropyron repens*) and marsh foxtail (*Alopecurus geniculatus*)) or with a scattered distribution of sturdy individuals and patches confined to the coves at the head of Perseverance Harbour and Tucker Valley (zone 3 in Fig. 1). Many of the latter group are only found close to the shore (*Arrhenatherum elatius, Rumex* spp. and *Sonchus asper*), but others

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* This coincided with heavy flowering in many of the indigenous species, notably the snowgrass (this genus and many other alpine species are known to be florally induced and initiated in the summer prior to anthesis; Mark 1970), *Pleurophyllum* spp., *Stilbocarpa polaris, Hebe benthamii* and *Anisotome antipoda* a notoriously poor flowerer (Meurk 1975).

frequent the tracks leading away from the coves (sweet vernal, cocksfoot, catsear and *Juncus bufonius*) although catsear has not been seen as far afield as reported by Sorensen (1951). The common daisy (*Bellis perennis*) has also lost some ground and certainly Sorensen's (1951) annotation for sheep's sorrel: "plentiful all over the island and now very widespread" could not be upheld today. I have never seen it outside zone 3 (Fig. 1), but within that precinct it is probably one of the best established forbs, with its tall red inflorescences being particularly conspicuous in summer, even amongst the *P. litorosa* tussock.

The only members of this class found higher than 20 m above the shoreline are *S. asper* (30 m), sheep's sorrel (30 m), catsear (116 m), cocksfoot (137 m), dandelion (*Taraxacum officinale*) (120 m) and sweet vernal (330 m). The last two species could probably be placed in the "widespread" class, as they have both been recently discovered outside zone 3: the dandelion on the west slopes of St Col ridge near the fence line and sweet vernal in the heavily grazed meadow of the northern cirque of Mt Honey.

A number of these species (particularly grasses) appear to be resisting encroachment by the native plants although it is doubtful if many of this class will play a permanent role in the developing communities (e.g. *Lotus uliginosus, Lamium purpureum*). Marsh foxtail may hold its place as it is well adapted to the swampy places that abound on Campbell Island. It is already well entrenched around the top of Tucker Cove above the high-tide mark.

Widespread naturalized aliens (10 spp.)

All but brown top, *Poa pratensis, Poa trivialis* and pearlwort (*Sagina procumbens*) have definitely been known on the island since the early farming days (Laing 1909) and these were almost certainly there too, although in vegetative condition could easily have been overlooked. They are all widely distributed, at least south of the Azimuth-Fizeau saddle and west of Mt Lyall and Mt Honey, where the most intensive pastoral management was practised (zone 4, Fig. 1). Sixty percent were probably introduced intentionally and the rest are common seed contaminants which can survive passage through an animal's gut. Most of them now occupy the full breadth of the low alpine zone (*P. pratensis* up to 153 m, Yorkshire fog 183 m, common chickweed 284 m, pearlwort 284 m, chewings fescue 320 m) while some extend even higher (*Poa annua* 403 m, browntop 488 m, mouse-eared chickweed 546 m).

*Poa annua* and the two chickweeds are a remarkable trio. They were probably among the earliest colonisers, although they were not noticed by the undoubtedly overworked Hooker (1847). Macquarie Island was known to have supported these species around the shore by at least 1880 (Scott 1883). Furthermore, they are the only ubiquitous aliens in the subantarctic flora as a whole (Walton 1975), with one exception - the Snares Islands - for which *P. annua* and *Stellaria media* comprise the total adventive flora (Fineran 1969). On the mainland these same two species seed throughout the year (Healy 1973), a characteristic which has helped them in the

subantarctic, and makes up for any disadvantage in being annual. In any case *P. annua* may assume a perennial habit in adverse conditions.

Pearlwort and mouse-eared chickweed have become characteristic pioneers of abandoned albatross nests, alongside the native "weeds" *Acaena minor, Epilobium confertifolium, E. pedunculare, Luzula crinita, Neopaxia australasica* and *Stellaria decipiens*.

Most of the grasses are confined to the heavily cropped *Bulbinella* / turf meadows and track-sides, where chewing's fescue occasionally attains physiognomic dominance. The chickweeds, pearlwort and *P. annua* are more common in open situations although *C. holosteoides* is by far the most consistently distributed adventive, being present over the entire island.

White clover is the only doubtful member of the "widespread" group. I cannot recall having seen clover beyond occupation sites and the Camp Cove and Garden Cove swards, although Sorensen (1951) remarked that clover was "plentiful on all drier parts of the island". Bailey and Sorensen (1962) said it was common in tussock grassland, and Wilson and Orwin (1964) reported it to be common only on the northeast slopes of Mt Dumas. Leaf cuticles of white clover, sweet vernal and sheep's sorrel were found in the rumens of sheep killed in the St Col-Azimuth area (Hercus in Wilson and Orwin 1964). None of these species have been seen recently in this area and, although scattered populations may be overlooked easily, they are obviously less common than they once were.

## II PALATABILITY OF SOME NATIVE PLANTS, TO SHEEP

Table 2 summarises the results of the experiment described in the introduction. Relative feeding frequencies observed during four subequal time intervals are shown together with the percent fresh weight consumed, of each species, and this expressed as a percentage of the total herbage consumed. Statistical significance is quoted at the 5% level.

During "Time-1" *A. latifolia, C. antarctica, P. foliosa* and young fronds of *P. vestitum* were paid significantly more attention than *B. rossii*. In "Time-2" *P. foliosa* was browsed more intensely than all other species, but in "Time-3" was significantly favoured over *P. litorosa* and *B. rossii* alone. Although an analysis for "Time-4" could not be performed, the much larger value for *P. litorosa* is indicative of the reduced availability of the more palatable species as these were consumed or rendered inedible. For example, leaf stalks of *A. latifolia* were eaten less enthusiastically than the blades. The freshweight consumption of the species reveals that young fronds of *P. vestitum* and foliage of *P. foliosa, C. antarctica,* and *A. latifolia* are eaten in preference (the latter two non-significantly) to *P. litorosa, P. vestitum* (old fronds) and *B. rossii*.

TABLE 2. RESULTS OF SHEEP FEEDING EXPERIMENT TO TEST THE PALATABILITIES OF SIX IMPORTANT CAMPBELL ISLAND PLANTS; INDICATING FEEDING FREQUENCY DURING FOUR SUBEQUAL TIME INTERVALS, PERCENT FRESH-WEIGHT OF EACH SAMPLE CONSUMED AND THIS EXPRESSED AS A PERCENTAGE OF TOTAL CONSUMPTION. STANDARD DEVIATIONS DERIVE FROM 4 REPLICATES. (y) = young fronds; (o) = old fronds.

| | *Polystichum vestitum* (y) | *Poa foliosa* | *Chionochloa antarctica* | *Anisotome latifolia* | *Poa litorosa* | *Polystichum vestitum* (o) | *Bulbinella rossii* |
|---|---|---|---|---|---|---|---|
| Feeding frequency | | | | | | | |
| Time-1 | 18.3 ± 7.5 | 20.9 ± 15.6 | 20.4 ± 12.9 | 21.9 ± 10.1 | 11.4 ± 19.7 | 5.6 ± 4.5 | 1.3 ± 2.5 |
| Time-2 | 13.3 ± 7.2 | 41.4 ± 14.7 | 8.8 ± 6.7 | 5.4 ± 8.2 | 12.1 ± 9.2 | 14.0 ± 8.7 | 4.5 ± 6.4 |
| Time-3 | 19.7 ± 16.4 | 36.9 ± 26.5 | 9.1 ± 11.5 | 11.4 ± 9.2 | 5.6 ± 9.6 | 12.5 ± 12.4 | 4.9 ± 4.3 |
| Time-4 | 4.7 | 20.9 | 14.0 | 7.0 | 48.8 | 2.3 | 2.3 |
| Mean | 14.0 | 30.0 | 13.0 | 11.4 | 19.5 | 8.6 | 3.3 |
| Consumption | | | | | | | |
| % of species | 56.4 ± 4.8 | 54.2 ± 10.9 | 40.4 ± 10.1 | 35.9 ± 2.0 | 30.0 ± 14.7 | 25.3 ± 20.3 | 10.0 ± 9.4 |
| % of total | 24.5 ± 2.4 | 21.1 ± 2.2 | 15.6 ± 2.5 | 14.3 ± 2.7 | 11.3 ± 3.6 | 9.1 ± 5.2 | 4.2 ± 3.8 |

## DISCUSSION

### GENERAL

The criteria used here in bestowing "widespread alien" status are more conservative than in Walton and Smith's (1973) treatment. When classifying time-dependent phenomena, criteria must be adjusted relative to the time of observation. This is pertinent to consideration of those "restricted" species found commonly around the top of Perseverance Harbour (*Arrhenatherum elatius*, cocksfoot, sweet vernal, catsear, *Ranunculus repens* and 3 *Rumex* spp.). If an alien had spread this far on South Georgia one would probably have no hesitation in discriminating between it and those "restricted naturalized" aliens growing within a hundred metres of abandoned buildings, but on the milder Campbell Island faster rates of migration could be misinterpreted. Moreover "widespread" aliens in South Georgia owe their geographical spread to initial establishment at past settlements scattered along the extensive coastline, whereas on Campbell Island this class encompasses species broadcast intentionally as seed as the vegetation was opened up. This better start given to Campbell Island aliens towards invasion of the hinterland, must be considered when comparing categories with other places.

The development of an alien florula and its segregation into distributional categories, may be understood in terms of a species pool upon which selective filters operate progressively; first in relation to dispersal mechanisms and vector availability, then to physiological amplitude, reproductive strategy and competitive prowess. The success of a species in negotiating the filters defines its niche within the hierarchy of alien classes.

The potential sources of Campbell Island's introduced plants include the floras of Europe, North America, Australasia and perhaps Japan. The spread of plants with appropriate dispersal mechanisms might be virtually unlimited when humans are vectors. Although Salisbury (1961) concluded that most species can stowaway in mud, seed mixtures etc., there are no data on the total number of species' propagules that have reached Campbell Island's soil. Nearly all the alien species recorded on the subantarctic islands are well known European weeds, with some interesting exceptions related to local histories (Smith 1973, Walton and Smith 1973, this paper's reference to N.Z. introductions). In any event the vast majority of the total pool has failed to disperse to remote places ("non-dispersors", Table 3). Species which do, but which cannot tolerate the new physical environment, likewise never achieve membership of the localities species list ("non-germinators", Table 3).

Those seeds which germinate and grow ("germinators", Table 3), but which cannot compete or reproduce successfully (self sterile annuals with special pollination requirements) may appear from time to time as "transient aliens", which qualify for the species list. Better adapted species ("reproducors", Table 3) may persist for several years until overwhelmed by competitive pressures, unless succession is inhibited and a disclimax maintained. These are the "persistent aliens" which remain as legitimate members of the flora only so long as they

TABLE 3. NUMBERS OF INDIGENOUS SPECIES AND ALIENS, AS CLASSIFIED FROM SOUTH GEORGIA AND CAMPBELL ISLAND, PRESENT IN THE SUBANTARCTIC AND OTHER NEW ZEALAND OFFSHORE ISLANDS. CI = Campbell Island, AI = Auckland Islands, M = Macquarie Island, S = Snares Islands, W = Women's Island, MT = Muttonbird Islands, SG = South Georgia, PE = Prince Edward and Marion Islands, C = Crozet Islands, K = Kerguelen Island, A = Antarctica. Values in brackets include actual or estimated numbers of cultivated vegetables.

The segregation hierarchy of aliens is composed of: non-dispersors (d-), dispersors (d+), germinators with a physiological tolerance of environment (g), reproducors (r), successful competitors (c) and true naturalized species able to disperse freely within target region (n).

| | CI | AI | M | S | W | MT | SG | PE | C | K | A | COMPOSITE | SEGREGATION HIERARCHY |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Indigenous spp. | 128 | 187 | 36 | 19 | 43 | 85 | 26 | 25 | 28 | 29 | 2 | c.320 | |
| Alien spp. total | (81) | (38) | 4 | 7 | 12 | 27 | (59) | 13 | 11 | (38) | 7 | c.139 | |
| "widespread" | 12 | 11 | 3 | 3 | 4 | 8 | 12 | 7 | 7 | 8 | 2 | 13 | n |
| "restricted" | 17 | 9 | 0 | 2 | 2 | 7 | 9 | 2 | 0 | 4 | 0 | 20 | c |
| "persistent" | 23 | 4 | 0 | 2 | 2 | 3 | 18 | 1 | 1 | 2 | 0 | 35 | r |
| "transient" | (29) | 10 (14) | 1 | 0 | 4 | 9 | 15 (20) | 3 | 3 | 19 (24) | 5 | c.71 | g |
| "dispersors" | | | | | | | | | | | | c.100's | d+ |
| "non-dispersors" | | | | | | | | | | | | c.1000's | d- |

persist. Thus a need arises to distinguish between a species list and a florula. The place of these two species' classes is dependent on the continual artificial disruption of encroaching vegetation and/or continued introduction of seed.

Alien species which are adequate or strong "competitors" (Table 3), but which lack effective dispersal mechanisms or agents, comprise the "restricted naturalized alien" class. Those species which have spread into and become reproducing parts of natural communities are termed "widespread naturalized aliens". These two classes are quasi-permanent members of the regional flora, although in some cases they remain dependent on natural perturbation of the environment.

A total of 139 alien species (germinators) have been recorded from the subantarctic islands as a whole (Greene and Walton 1975, Johnson and Campbell 1975, Johnson 1976, Johnson pers. comm., this paper). Although this number can be expected to increase, the most important have probably made their appearance. If one combines the potentials demonstrated by the exhaustively studied alien species of South Georgia and Campbell Island, a general picture emerges of how "germinators" are further segregated in the subantarctic (Table 3). Seventy-one transients have been selected against as they were not reproductively viable and 35 persistent aliens have been filtered out as they were not competitive. Twenty restricted aliens have been screened from

the pool as they are neither competitively aggressive nor actively dispersive. This leaves 13 widespread naturalized aliens with assured places in southern floras.

A comparison of the southern islands in Table 3 reveals that all those that are large and environmentally diverse include at least half of the "widespread" species in their florulas, and their total number of aliens is of the same magnitude order as that of their indigenous floras. The exception of Macquarie Island is surprising in view of its long history of occupation and animal disturbance.

The only South Georgian naturalized species not found on Campbell Island are *Deschampsia caespitosa* and some Scandinavian arctic/alpine derivatives. Conversely, South Georgia does not support Yorkshire fog, sweet vernal nor catsear, and common chickweed is listed only as transient. These minor disparities are probably attributable to the relative importances of mineral and peat soils on the different islands. Sheep's sorrel, *Hieracium* spp., catsear and sweet vernal are the most widespread adventives on New Zealand mainland alpine soils, but they have lesser roles on the subantarctic peats. Mouse-eared chickweed and brown top are, however, common to both situations. Other differences are probably related to the rather more rigorous "high alpine" environments of most of the quoted islands, which contrasts with the low to sub-alpine habitats that dominate New Zealand's subantarctic outliers. Also since most of the traffic to these latter islands comes via Australasia, any European derived aliens will have been twice screened. In contrast, the more direct routes between European ports and other subantarctic islands opens them up to introductions inconceivable in the New Zealand context. A good example is the common boreal grass *Nardus stricta* which has found its way to both South Georgia and New Zealand (Healy, 1973), but the chances of this rare New Zealand alien being transported further south are remote.

All the widespread aliens of Campbell Island are extant on the Auckland Islands, though chiefly restricted to the grazed swards of Enderby and Rose Islands, but only a few species from the other categories are still present. This is not surprising because compared with Campbell Island modification was less extensive and not as prolonged, settlement was less continuous and fewer collectors visited at historically critical times. Since there are so many short-lived exotics, many undoubtedly escaped detection because no trained person recognised or collected them.

Equivalent to the "non-weed" introductions into South Georgia from Europe and South America, there are a small number of New Zealand natives that are disjunctly distributed (i.e. are absent from the Auckland Islands), were discovered only recently on Campbell Island and are very localized in open communities. Brockie (1948) postulated that these were unintentional introductions from the mainland. They include *Acaena* cf. *anserinifolia, Blechnum penna-marina, Gonocarpus aggregatus, Brachycome radicata, Cotula dispersa, Craspedia uniflora, Rumex flexuosus* and *Uncinia divaricata* (Meurk 1975). Although the first three species have been found recently on the Auckland Islands (Johnson and Campbell 1975), they are probably recent arrivals there too. In view of the circumpolar distribution

of *B. penna-marina* and the importance of *C. uniflora* in the closed high alpine wet rush-herbfields of Campbell Island, it would however seem unlikely that they were adventive. It has already been suggested that about six species of the Auckland Islands' flora may be adventive mainland indigenes (Ibid).

ALIEN STRATEGIES

Many of the successful aliens probably achieved their initial wide distribution through broadcast as pasture plants or as contaminants of the seed (G, C notation in Table 1) whereas most transients and persistents probably came in on clothes and boots, hair and hoof and in garden soil (Sorensen 1951, Salisbury 1961). Circumstantial evidence pointed to seeds of ryegrass, *Vulpia bromoides*, and *Bromus brevi-aristatus* having come in with tents and clothes belonging to the 1970 party (Meurk 1975). All these are indicated by an "H" notation in Table 1.

A few plants have possibly been introduced by birds or mammals. Although evacuation of the digestive system can be delayed up to 10 days after ingestion by cattle (Salisbury 1961) it is more likely that animal dispersal has been more important in facilitating spread on the island (notation "I" in Table 1). This seems likely for the chickweeds, *P. annua*, pearlwort, *Rumex* spp., *Ranunculus repens*, *Plantago lanceolata*, self-heal and dandelion (all of which may survive passage through the gut as seed, Salisbury 1961) and tutsan which has a fleshy fruit. Only the putative New Zealand introductions (*Acaena* and *Uncinia* spp.) have obvious adhesive adaptations such as hooks or spines.

The strong westerly winds may provide an effective aid to dispersal, although as yet no clear west to east migration paths have been discerned.

Plants may appear spasmodically long after the original source of contamination has disappeared. This is often due to seed longevity which may be enhanced in cold soils. Sheep's sorrel and catsear are known for their long-lived seed (Salisbury 1961) and the curious occurrences of *P. lanceolata* and foxglove might be explained by similar properties.

The physiological successes of the large pool of sub-antarctic aliens may be understood by examining the tolerances they display in their homeland. Salisbury (1961) stated that *Fumaria officinalis*, *Geranium pusillum*, *Solanum nigrum*, *Veronica persica* and *Anagallis arvensis* fail to reach 300 m altitude in Britain, and all these are transients on Campbell Island. However, the great majority of plants being considered here are commonly found above 460 m. Sheep's sorrel, pearlwort, *Cardamine hirsuta*, *P. annua*, *R. repens*, *Bellis perennis*, mouse-eared chickweed, yarrow and brown top are notable for being able to grow at altitudes above 1000 m in the British Isles which indicates tolerance of both cold climate and acid soil. On the other hand many of the same species display a remarkable plasticity, being also found in well drained, even drought-prone, situations (Healy 1973).

Many transient annuals fail because they are unable to flower or set seed in such hostile conditions. In contrast, vegetative growth of persistents can often be exceedingly vigorous in the high humidity and equable temperatures.

Achievement of flowering does not necessarily culminate in successful seeding. Twitch, possibly some of the legumes, and members of the Scrophulariaceae and Labiatae are self sterile. While dandelion is apomictic and *C. hirsuta* cleistogamic other entomophilous species may fail through lack of a suitable pollen vector. Long tongued bees are absent from Campbell Island, though lepidopterans, beetles and flies abound. Mulligan (1972) found that introduced entomophilous plants are usually readily pollinated by indigenous insect faunas. The dominance of anemophilous, autogenous or diptero-entomophilous plants within the adventive flora is striking. Of 28 naturalized species, five composites, three Polygonaceae, three Caryophyllaceae and *R. repens* can all be pollinated by flies or may self pollinate. Another 12 species are grasses and rushes. The exceptions are white clover, *Lotus, Mimulus,* perhaps selfheal (Meurk 1975) and flax (bird pollinated). The legumes are often considered obligately hymenophilous, but even these species may modify their strategies and become self fertile in remote and suboptimal environments (Proctor and Yeo 1973). However on Campbell Island they probably depend upon vegetative propagation. The present scattered dispersion of clover is a consequence of its initial broadcast from seed by the pioneer farmers, and its recent decline due to its failure to reproduce sexually.

Mulligan and Findlay (1970) demonstrated that among 65 Canadian weeds, 13 of which are common to Campbell Island, all 33 annuals and 21 of 23 biennial and caespitose perennials set viable seed when the flowers were bagged to prevent cross pollination. They concluded that the self-fertile and agamospermic strategies or vegetative prowess were important weed adaptations and Baker (1955) pointed to the significance of these characters to survival in plants which experience long distance dispersal.

## THE DEFENSIVE STATUS OF THE NATIVE FLORA

There has never been a substantiated extinction of a native species on Campbell Island despite the catastrophic effects of farming on the low alpine tussock and the present restriction to refugia of many of the palatable megaherbs and grasses. Nevertheless, there are a few very localized indigenes which have probably been on the island a relatively short time. Some of these, such as *Rumex neglectus, Poa novae-zelandiae, Lycopodium* cf. *australianum, Tmesipteris tannensis, Acianthus viridis* and *Epilobium pernitens,* are possibly threatened as much by botanists as sheep.

In an unmodified or closed community naturalized plants are very uncommon. This is demonstrated by the sharp contrast between the total absence of adventives on a tracked low alpine cushion-bog on the former sheep holding area of Homestead Ridge, and the impressive assemblage of 19 species in the adjacent better drained tussock-meadow.

Factors which have mitigated against replacement of the native species by adventives are:

a) the resilience of some components of the indigenous flora which is a consequence of their inability to carry fire and/or their low palatabilities,

b) the rocky cliff-bound terrain, which affords extensive refugia for escape from fire and grazing,

c) the frequent inclement weather which hindered burning activities (Spence 1968),

d) the superior adaptations of the native plants to the peculiarities of their own physical environment (the blanket peat substrate) and,

e) the large number of natives which occupy "weed" or pioneer niches. These are of significance in colonisation of fresh peat slips, abandoned bird nests, penguin rookeries and sea elephant wallows (perhaps 38 spp.).

Thus a large proportion of the native flora is capable of strongly resisting invasion, even after disturbance. This contrasts with Holdgate and Wace's (1961) general observations on the extensive damage to the native biota of the circum-polar islands, which they attributed to:

1) the small native floras
2) the absence of important continental animal and plant groups (e.g. herbivorous mammals, gymnosperms), which results in a vegetation sensitive to grazing and an avifauna sensitive to predators,
3) species adapted to weak competition and selected primarily for dispersal capacity,
4) the limitations placed on endemism by Pleistocene glaciation, and finally,
5) the tendency of these islands to have few seral species.

Obviously all these generalisations do not apply to Campbell and the Auckland Islands. Rather they apply best to islands of subtropical or warm-temperate climates. In contrast the colder islands do not seem in great danger of being overwhelmed by exotic species. It is the continued presence of introduced grazing mammals that poses the most serious threat (Walton 1974), not so much to the flora as to the integrity of the native plant communities. On both the Auckland Islands and on Campbell Island it is the native weedy species that dominate even the disclimactic *Bulbinella*/turf meadows (Wilson and Orwin 1964, Taylor 1971, Johnson and Campbell 1975). It is gratifying that this present situation is quite the reverse of the dire predictions made by Cockayne (1903), after he had examined the early effects of farming.

## TRENDS IN THE VEGETATION; PAST, PRESENT AND FUTURE

I have already attempted to show the relationship of induced vegetation changes, to the influx and eventual ecological segregation of exotic species (Fig. 2). Most alien species recorded (Table 1) had probably made transient appearances by the end of last century although perhaps only the chickweeds, *P. annua* and the planted flax were secure. They accompanied localised disturbances which have been frequent and which are likely to continue indefinitely. The future situation will differ with regard to the variety of potential introductions which will increase gradually as more European plants become better established in New Zealand (Campbell Island's direct source).

As has been stressed repeatedly, it was farming that affected the vegetation most radically. Fire, hungry stock and the only important conscious injection of seed allowed invasion of the hinterland by proven pasture species and hardy weeds alike, with the naturalized aliens of Table 1 predominant.

The native vegetation suffered when pristine dominants like *P. foliosa, C. antarctica, Anisotome* spp., *Pleurophyllum* spp., *Stilbocarpa polaris* and young fern fronds suddenly proved to be highly palatable, especially after burning (Table 2). This explains why less favoured species such as *B. rossii* and *P. litorosa* are now physiognomically dominant over wide areas. It is interesting, however, that sheep definitely prefer variety to an unrelieved diet of even their most cherished fodder, as demonstrated by their deliberate sampling of all species during the feeding experiment (Table 2). Wilson and Orwin (1964) described similar behaviour and noted that *B. rossii* fragments were sometimes found in rumen samples. I have observed sheep chewing the white fleshy bases of this species which suggests they may be deriving fresh water from this source. Even *P. litorosa* and the old harsh *P. vestitum* fronds were attacked vigorously at times, as indicated by the large standard deviations in the consumption results (Table 2). The consistently high palatability of young *P. vestitum* fronds undoubtedly accounts for the "rafts" of dead fern rhizomes especially common in areas of intense sheep and cattle grazing.

Only the most aggressive aliens (Table 1) have spread to the least modified eastern parts of the Island (zone 5 in Fig. 1). However once farming had collapsed declining stock densities allowed a secondary succession (probably retarded between 1960-70 with the sheep population growing in response to a warming climate) in which exotic pasture grasses played a major role. The complete elimination of sheep in the north (1970) allowed these grasses to grow profusely (the north St Col ridge now supports swards of chewing's fescue and *Poa* spp. up to 0.5 m tall). Furthermore, many of the palatable native species have started to reoccupy formerly relinquished territory, a process which would be extended over the whole island once all stock were removed.

The gradual transformation of induced tussock/*B. rossii* meadows back towards the climax tussock/scrubland will, however, result in new vegetation patterns. The climatic amelioration since the "Little Ice Age" (Salinger and Gunn 1975) may cause vegetation zones to climb perhaps 100 m above former levels so that woody vegetation will become more prominent than in the immediate past. The destruction of the low alpine snow-grass has merely accelerated this trend. Photographic records testify to the rapid spread, since 1945, of *Dracophyllum* spp. up to 200 m. Zotov (1965) speculated that seedlings of these shrubs could not establish in dense shade (this is certainly the case under "dwarf forest" canopies), which accounts for the slow encroachment of shrubs into dense undisturbed tussock.

A long term perspective shows that these changes are cyclical in nature. This is demonstrated by the occurrence of subfossil wood in peat at elevated or exposed sites on both Campbell (pers. obs.) and Auckland Islands (Godley pers. comm.) and from pollen diagrams that indicate an earlier woody peak in the subantarctic (Moar 1958), perhaps up to about 4000 years B.P.

As the succession continues the exotic flora will probably become increasingly excluded from the mature communities, and will remain largely at sites of natural and induced disturbance. We are presently witnessing the active segregation of the "naturalized" flora, the consequences of which will determine the final status of many aliens. Already white clover, Yorkshire fog and sweet vernal appear to be losing ground.

## CONCLUSIONS

At present there is a sub-linear inverse relationship between alien class status and class size (i.e. the most successful classes have the fewest species, Table 3). However, I suspect that given isolation from disruptive forces, the resulting steady state vegetation will have fewer naturalized species than currently recognized. This will skew the relationship towards the "transient/persistent" classes. In this eventual hypothetical state most "restricted" and perhaps some "widespread" naturalized species would drop to persistent status. This could mean that the "restricted" category is artificial (or is a function of artificial disturbance) and will ultimately disappear.

Of the 81 adventive species considered here I would predict that only the "widespread" aliens, minus *Trifolium repens* and *Holcus lanatus*, but with the addition of *Alopecurus geniculatus, Hypochaeris radicata, Sonchus asper, Anthoxanthum odoratum, Dactylis glomerata, Phormium tenax* and possibly *Taraxacum officinale, Ranunculus repens*, three *Rumex* spp. and *Juncus bufonius* will maintain permanent places in the natural vegetation. Walton and Smith (1973) classed *T. officinale, R. repens, Agropyron repens, Rumex acetosella* and *Achillea millefolium* (among others not represented in the New Zealand region) as naturalized in the more rigorous conditions of South Georgia, which suggests that these species may have a potential as yet unrealised on the New Zealand subantarctic islands. Of the nine species considered worthy of mention by Walton (1975), but not as yet recorded on Campbell Island, only *Deschampsia caespitosa* seems capable of finding a future niche there. The only species that might endanger the integrity of the future vegetation would be broom (*Sarothamnus scoparius*) which has demonstrated some potential to spread when left unchecked, although lack of suitable pollinators might preclude any real threat.

Thus a possibly exaggerated estimate of the future role of alien plants in Campbell Island's ecosystem is that about 24 species will become fully naturalized, although two-thirds of these will be restricted (ecologically, not geographically) to naturally perturbed habitats or littoral communities. *Cerastium holosteoides, Festuca rubra, Agrostis tenuis, Poa pratensis* and *Poa trivialis* could be successful in tussock grasslands; *Poa annua, Sagina procumbens* and *Stellaria media* in seral situations and *A. geniculatus* and *J. bufonius* in marshy places, the other 14 species could fill gaps in the littoral fringe. The remainder of the "restricted" class would be relegated to a "persistent" category which would then number about 28 species while the number of transients would remain at 30 plus. Some of the newly constituted persistent class would continue to occupy

ground (on a rotation) in the environs of encampments, and any of the transient species could make sporadic appearances.

The number and nature of the alien species in a flora should reflect some intrinsic attributes of the environment, if we assume a constant source pool of species and equal opportunity for dispersal. Although South Georgia has a larger source pool than the New Zealand subantarctic islands, or conversely fewer impediments to dispersal, it is probable this island will end up with something less than 20 naturalized species comparing with Campbell Island's projected 24. This helps define empirically the respective target environments, although care must be taken, in comparing different biogeographic regions, that the time factor is not compounded with environmental severity.

As South Georgia is larger and has a greater source pool, we can say tentatively that the size, diversity and spread of its alien flora reflect more severe conditions than on Campbell Island. This is consistent with the climatological evidence available and the zonal interpretation of their respective vegetations I have presented here.

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